



UvA-DARE (Digital Academic Repository)

The stochastic demography of two coexisting male morphs

Smallegange, I.M.; Coulson, T.

Published in:
Ecology

DOI:
[10.1890/09-2069.1](https://doi.org/10.1890/09-2069.1)

[Link to publication](#)

Citation for published version (APA):

Smallegange, I. M., & Coulson, T. (2011). The stochastic demography of two coexisting male morphs. *Ecology*, 92(3), 755-764. <https://doi.org/10.1890/09-2069.1>

General rights

It is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), other than for strictly personal, individual use, unless the work is under an open content license (like Creative Commons).

Disclaimer/Complaints regulations

If you believe that digital publication of certain material infringes any of your rights or (privacy) interests, please let the Library know, stating your reasons. In case of a legitimate complaint, the Library will make the material inaccessible and/or remove it from the website. Please Ask the Library: <https://uba.uva.nl/en/contact>, or a letter to: Library of the University of Amsterdam, Secretariat, Singel 425, 1012 WP Amsterdam, The Netherlands. You will be contacted as soon as possible.

The stochastic demography of two coexisting male morphs

ISABEL M. SMALLEGANGE¹ AND TIM COULSON

Division of Biology, Imperial College London, Silwood Park, Ascot SL5 7PY United Kingdom

Abstract. If genetically distinct morphs coexist under a range of natural conditions, they should have equal long-run fitnesses across a wide range of different stochastic environments. In other words, the sequence and frequency of good and bad environments should not substantially impact long-run growth rates. When different morphs have contrasting life histories that vary with environmental conditions, however, it seems improbable that growth rates can be equivalent across a range of stochastic environments without invoking a strong stabilizing mechanism to explain their persistence. As yet, there has been no research characterizing the long-run stochastic growth rate (λ_s) of different morphs across a wide range of stochastic environments. Assuming density independence, we show that the two genetic male morphs in the bulb mite (*Rhizoglyphus robini*)—fighters, which are able to kill other mites, and benign scramblers—have similar λ_s in different Markovian environments (different simulated random sequences of good and bad habitats). Elasticity analyses revealed that λ_s was most sensitive to perturbation of adult survival rate. A slight (biologically and statistically realistic) increase in scambler adult survival equalized scambler and fighter λ_s . The fitness equivalence of the two morphs suggests that stabilizing mechanisms, such as density or frequency dependence, required to maintain their coexistence, are weak. We advocate that stochastic demography can offer a powerful approach to identify and understand the circumstances under which genetic polymorphisms can be maintained in stochastic environments.

Key words: *alternative reproductive phenotype; environmental variation; genetic male dimorphism; Markov chain; stage-structured population projection matrix.*

INTRODUCTION

Identifying conditions for the coexistence of different genetic morphs within populations contributes to answering a key question in population biology: what maintains genetic diversity? Classical models in evolutionary theory state that for different genetic morphs to coexist, their mean fitness must be equal over time (Slatkin 1978, Gross 1996). This has been tested for natural populations, assuming constant environmental conditions (Shuster and Wade 1991). However, in nature, different populations of the same species likely experience different stochastic regimes (Tuljapurkar 1990). From these classical models (Slatkin 1978, Gross 1996) it follows that for coexistence to occur in different populations, the fitnesses of different morphs must be statistically indistinguishable in the long-run (although coexistence may occur only under certain sequences and frequencies of different environmental conditions). To our knowledge, there has been no research characterizing the long-run growth rates of different morphs across different stochastic environments. In density-independent stochastic environments, fitness in relation to vital rates such as survival and reproduction is measured by

the long-run stochastic population growth rate (Cohen 1977, Tuljapurkar et al. 2003). Here, we test the hypothesis that genetically distinct morphs have statistically indistinguishable long-run stochastic growth rates across a range of stochastic environments. Long-term coexistence of morphs with statistically indistinguishable stochastic growth rates, however, likely requires stabilizing mechanisms such as density- or frequency-dependent selection (Gross 1996, Chesson 2000, Adler et al. 2007). Yet, the appropriate growth rate to use to describe outcomes in density- and frequency-dependent environments is context dependent (Metz et al. 1992, Metcalf and Pavard 2007), greatly complicating analyses of coexisting morphs. Therefore, for now, we resort to density-independent demographic models, which may under certain circumstances provide adequate approximations when density or frequency dependence operates (Caswell 2001).

The benefit of using density-independent, stochastic demographic methods is that it allows us to explore whether weak or strong stabilizing mechanisms are required for the maintenance and long-term coexistence of different, coexisting genetic morphs. Recent theoretical work shows that the strength of stabilizing mechanisms such as density or frequency dependence (Gross 1996) or a storage effect (Chesson 1994) depends on the degree of fitness equivalence (Chesson 2000, Adler et al. 2007). Specifically, if different genetic

Manuscript received 5 November 2009; revised 30 April 2010; accepted 26 July 2010. Corresponding Editor: S. J. Schreiber.

¹ E-mail: i.smallegange@imperial.ac.uk

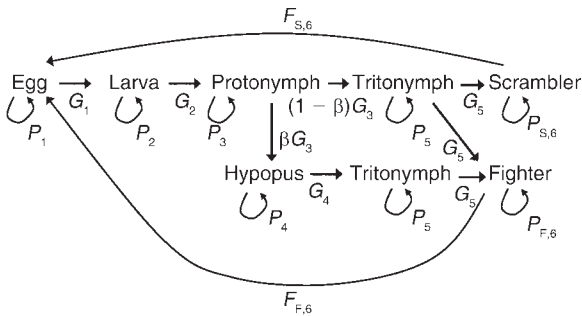


FIG. 1. Life cycle of fighter and scambler bulb mites. Mites that went through the hypopus stage always developed into a fighter. The survival rate P_6 and the fecundity rate F_6 differed between scamblers (subscript S) and fighters (subscript F; Appendix). G_i stands for the probability of surviving and growing into the next stage.

morphs have similar stochastic growth rates, then coexistence can be maintained by weak stabilizing mechanisms (Chesson 2000, Adler et al. 2007), characterized by a near-zero slope of the relationship between fitness and relative frequency of each morph in the population (Adler et al. 2007). Yet, if large differences in stochastic growth rates exist between the different morphs, this would indicate that strong stabilizing mechanisms are needed to overcome the large fitness differences (Chesson 2000, Adler et al. 2007), and fitness functions are characterized by a negative slope of the relationship between fitness and relative frequency of each morph in the population (Adler et al. 2007). This novel demographic approach has obvious utility in understanding how environmental change could impact genetic diversity within polymorphic populations (Boyce et al. 2006). It may also inform on whether genetic diversity can be maintained through fluctuations in the stochasticity of the environment if the relative fitnesses of different genetic morphs vary with the color of environmental noise (so called stochastic-environment-dependent selection).

We explore our premise for male bulb mites (*Rhizoglyphus robini*), which show two distinct morphs: heteromorphic males or “fighters” are armed with a thickened and sharply terminated third pair of legs which they can use to kill other males (Radwan et al. 2000), whereas homeomorphic males or “scramblers” have unmodified legs and are defenseless (see Plate 1). Apart from these morphological differences, the only other reported difference between the two morphs is that scamblers live longer than fighters (Radwan and Bogacz 2000). Why the two morphs coexist still puzzles biologists (Radwan 2007), mainly because scamblers always seem to be worse off as they, unlike fighters, are unable to kill rival males and monopolize access to females (Radwan et al. 2000, Radwan and Klimas 2001). The expression of male morph in the bulb mite is partially genetically determined (Radwan 1995). Here, we first aim to confirm that heritability of male morph is

a general feature in the bulb mite. Because male morph expression can also depend on the environment (Radwan 1995), we also assess experimentally if this is the case for bulb mites in our experimental system. In the same experiment, we investigate the expression of a facultative dispersal morph (the hypopus) in relation to environmental quality and male morph. The experimental data, together with data from existing literature (Capua and Gerson 1983, Gerson et al. 1983, Radwan and Bogacz 2000) form the basis for constructing life tables for scamblers and fighters. From the life tables, we create a stochastic demographic model by constructing population projection matrices (PPMs) for fighters and scamblers living in two kinds of habitat: a high-food-quality and a low-food-quality habitat.

Using the stochastic demographic model we calculate stochastic growth rates of fighters and scamblers across a range of different stochastic environments, i.e., different sequences of good and bad habitats. In nature, bulb mites forage on high quality subterranean parts of plants such as bulbs and tubers (Diaz et al. 2000). Mite populations in high quality habitats rapidly increase in size, eventually utilizing the resource, upon which mites have to feed in low quality habitats until a new high quality habitat is discovered. Thus given that different populations of mites likely experience different environmental regimes, we might expect coexistence to be possible across a range of stochastic environments. By means of perturbation analysis we investigate the circumstances under which the stochastic growth rates of the coexisting male morphs are statistically indistinguishable.

METHODS

Heritability of male morph expression

We set up fighter and scambler lines (Appendix) and estimated heritability of male morph expression after five generations of selection using the so-called threshold model of quantitative genetics (Falconer 1989; Appendix). According to this model a continuously and normally distributed character, called liability, underlies the dimorphic variation, and the phenotypic expression of the variation is the result of a threshold. Individuals above the threshold develop into one morph, whereas individuals below the threshold develop into the other morph.

Life tables

The life cycle of the bulb mite consists of six stages (Fig. 1): egg, larva, protonymph, hypopus (also called deutonymph), tritonymph, and adult. The hypopus is a facultative dispersal stage to escape unfavorable environmental conditions and its development is induced by low food quality and quantity (Diaz et al. 2000). We constructed life tables for mites in a high-quality-food habitat (ad libitum access to yeast) and a low-quality-food habitat (ad libitum access to filter paper), which we will respectively refer to as the good and bad habitat.

TABLE 1. Conditions of the good and bad habitat in this study and previous studies of which we used the results to construct the survival and fecundity functions for mites in the good and bad habitat.

Sex	Good habitat		Bad habitat	
	Juvenile stages	Adult stage	Juvenile stages	Adult stage
Females	garlic, 27°C (1)	garlic, 27°C (1)	filter paper, 27°C (1, 3, 4)	filter paper, 27°C (4)
Males	garlic, 27°C (1)	yeast/wheat germ, 24°C (2)	filter paper, 27°C (1, 3, 4)	filter paper, 27°C (4)

Notes: Numbers in parentheses refer to references and are coded: (1) Gerson et al. (1983); (2) Radwan and Bogacz (2000); (3) Capua and Gerson (1983), and (4) life table experiments of this study. Gerson et al. (1983) present average stage durations, survival rates and fecundity curves (all without SEs); Radwan and Bogacz (2000) present survival plots for fighters and scramblers (without SEs); Capua and Gerson (1983) present average stage durations of hypopodes (without SEs).

Point estimates of fecundity and survival rates for females, fighters, and scramblers are available for the good habitat (Gerson et al. 1983, Radwan and Bogacz 2000), but not for mites living in the bad habitat (Table 1). To obtain estimates of these vital rates for adults in the bad habitat (we assumed that juvenile development of males and females does not differ), we conducted an experiment following the methods of Gerson et al. (1983). A hundred larvae from the stock cultures were put in individual 10 mm diameter glass tubes with ad libitum access to yeast. Upon maturation, 12 mating pairs where the male was a fighter and 12 mating pairs where the male was scrambler were formed and were each put in a 3-cm Petri dish and given ad libitum access to filter paper. Each couple remained together throughout life and survival and fecundity of males and females were recorded daily. Mites were kept in an incubator at a constant temperature of 27°C and >70% relative humidity.

In a second experiment we estimated the probability that a protonymph survives to grow into either a hypopus or directly into a tritonymph, and also tested if male morph expression (i.e., the proportion of male offspring that are scramblers) differed between mites that developed in the different habitats. A detailed description of the experimental methods is given in the Appendix. Briefly, eggs from each of 22 fighter mating pairs and from each of 22 scrambler mating pairs were put in Petri dishes with ad libitum access to yeast. Eggs from another 22 fighter mating pairs and 22 scramblers mating pairs were put in Petri dishes with ad libitum access to filter paper. Half of all dishes within each habitat treatment underwent a 24-h dry period. The experimental design therefore had three treatments: sire male morph (scrambler/fighter), habitat (good/bad), and dry period (yes/no). Each treatment combination was replicated 11 times. After mites developed into larvae, any hypopus found during the following 12 days was isolated to determine its sex and morph (hypopodes were given ad libitum access to yeast). Outside of this period hypopodes were scored but not isolated. The experiment finished once all eggs had developed into adults and their sex and morph was scored. We expressed the proportion of hypopodes as a fraction of the total number of mites in each Petri dish, and the proportion of scramblers as a fraction of the total

number of males in each Petri dish. Because we had only counted the number of males, we multiplied this number by two to obtain a total population count of each Petri dish. Observed sex ratios do not differ from 1:1 (Gerson et al. 1983) so our measure is representative of the whole population.

To conform to the assumption of density independence implicit in our stochastic demographic model, mites were kept in individual tubes during different experimental stages. Furthermore, to avoid density-dependent effects through exploitation competition, a likely mechanism to give rise to density dependence in this species (Lesna et al. 1996), we provided mites with ad libitum access to food in all experiments. Finally, previous studies have not found evidence for density- or frequency-dependent effects on the relative survival or mating success of the two male morphs under constant environmental conditions (Radwan and Klimas 2001) such as those in our experiments, fulfilling the assumption of density independence.

Stochastic demographic model

The long-run stochastic growth rate, λ_s , is calculated over a period of length T by taking the exponent of

$$\log \lambda_s = \frac{1}{T} \sum_{t=0}^{T-1} r_t$$

with $r_t = \log(\sum_i \mathbf{p}_i(t+1) / \sum_i \mathbf{p}_i(t))$ and $\mathbf{p}(t)$ is the population vector at time t . The stochastic demographic model is $\mathbf{p}(t+1) = \mathbf{A}(t)\mathbf{p}(t)$ where $\mathbf{A}(t)$ is a stage-classified PPM at time t defined by a Markov chain of habitat transition probabilities (see below). To parameterize each PPM, we first estimated the probability of growing from stage i to stage $i+1$, γ_i , assuming that the probability of growing into the next stage depends on the age distribution within the current stage. Assuming furthermore that the population is stationary (See Appendix: Figs. A2 and A3) and that the age distribution within stages is stable:

$$\gamma_i = \left[\left(\frac{\sigma_i}{\lambda} \right)^{T_i} - \left(\frac{\sigma_i}{\lambda} \right)^{T_i-1} \right] / \left[\left(\frac{\sigma_i}{\lambda} \right)^{T_i} - 1 \right]$$

where T_i is the duration of stage i (Table 2) and λ is the population growth rate. The daily survival probability in stage i , σ_i , equals e^{μ} , where $t = 1$ day and μ is the

TABLE 2. Average durations (days) of the different life stages of females, fighters, and scramblers.

Stage	Good habitat			Bad habitat		
	Females	Fighters	Scramblers	Females	Fighters	Scramblers
1 Egg	3.60	3.60	3.60	3.50	3.50	3.50
2 Larva	3.00	3.00	3.00	9.50	9.50	9.50
3 Protonymph	2.80	2.80	2.80	15.40	15.40	15.40
4 Hypopus				10.30	10.30	
5 Tritonymph	2.60	2.60	2.60	10.70	10.70	10.70
6 Adult	31.00	40.20	49.60	21.57	18.75	28.50

Notes: For references, see Table 1. Empty cells indicate that there are no observations for those cells.

constant force of mortality over each time step of one day (calculated by estimating the slope of the regression of log-transformed survival probability [d^{-1}] against age [d] using the survivorship functions [Appendix: Fig. A4; Caswell 2001]). Estimated daily survival probabilities are given in the Appendix. Estimating γ_i involves an iterative procedure where the entries into the PPM are calculated using an initial value of λ . The eigenvalues of the PPM yield the second estimate of λ with which the parameters are estimated again, until λ converges to four decimal places.

In terms of the parameters σ_i and γ_i , the probability of surviving and growing into the next stage (G_i), and the probability of surviving and remaining in the same stage (P_i) are $G_i = \sigma_i \gamma_i$, and $P_i = \sigma_i(1 - \gamma_i)$. The probability of mites developing from a protonymph into a hypopus is given by $\beta \times G_3$, and the proportion of individuals that grows from a protonymph directly into a tritonymph as $(1 - \beta) \times G_3$. The resulting stage-classified PPM takes the following form:

$$\begin{bmatrix} P_1 & 0 & 0 & 0 & 0 & F_6 \\ G_1 & P_2 & 0 & 0 & 0 & 0 \\ 0 & G_2 & P_3 & 0 & 0 & 0 \\ 0 & 0 & \beta G_3 & P_4 & 0 & 0 \\ 0 & 0 & (1 - \beta)G_3 & G_4 & P_5 & 0 \\ 0 & 0 & 0 & 0 & G_5 & P_6 \end{bmatrix}$$

The point estimate of vital rate F_6 for reproductive output was calculated using the stage-classified birth-flow formulation (Caswell 2001) because egg-laying occurs continuously: $F_6 = \sqrt{\sigma_1}(m_6 + P_6 m_6/2)$, where m_6 is the average offspring production in the adult stage. Because growth of mite populations is limited by the lifetime reproductive output (R_0) of females, and not of males, we scaled male R_0 so that R_0 of fighters and scramblers equaled that of females (assuming no reproductive senescence). Because scramblers live longer than fighters (Radwan and Bogacz 2000), this means that the daily rate of reproduction, F_6 , was lower for scramblers than for fighters. This normalization, however, did not result in equal growth rates of fighters and scramblers (see *Results*). The PPMs for scramblers and fighters in the good and bad habitat are given in the Appendix.

Habitat Markov chain

The habitat is in one of two states: good or bad. The probability distribution of habitat states at time t is described by a two-state Markov chain. If state 1 is the good habitat and state 2 is the bad habitat, the Markov chain transition matrix \mathbf{H} is

$$\begin{bmatrix} 1 - p & p \\ p & 1 - p \end{bmatrix}$$

where p is the probability of switching habitats. The autocorrelation of the habitat Markov chain ($\rho = 1 - 2p$), which shows the color of the environmental stochasticity, differs with different values of p . For illustrative purposes and simplicity we set the probability of moving from the good to the bad habitat equal to the probability of moving from the bad to the good habitat. In the Appendix we extend the results of our analyses for unequal probabilities of switching habitats (Appendix: Fig. A7). By iterating \mathbf{H} , a time series of length 100 000 (with an initial transient length of 1000 discarded) was generated (shortening the length of this chain did not qualitatively affect our results (Appendix: Fig. A6)). This sequence determined the habitat state that the population of each morph experienced at each time step. Given the habitat state at time t , $\mathbf{A}(t)$ is then filled using point estimates of the vital rates for that habitat. In that way a PPM is generated at each time (Tuljapurkar et al. 2003), which was stored with associated vectors of population structure and reproductive value for further analysis. Because in this specific case the probability of switching from the good to the bad habitat always equals the probability of switching from the bad to good habitat, the expected percentage of time spent in each habitat is 50%.

RESULTS

Heritability of male morph expression

Over five generations, the total selection differential (expressed in standard deviation units of liability) equaled 4.518 for scramblers and 1.237 for fighters (Appendix). The total response to selection over the total selection differential, i.e. the realized heritability, equaled for scramblers $1.872/4.518 = 0.41$ (Appendix).

Hence the estimated heritability of the underlying liability for the scrambler morph was 41%. For fighters, the total response to selection differential equaled $0.347/1.237 = 0.30$ (Appendix) giving an estimated heritability of the underlying liability for fighter morph of 30%. The change in the fraction of scamblers over the course of five generations of selecting for fighters or scamblers is given in the Appendix (Fig. A1).

Adult survival and fecundity in the bad habitat

Age-specific survivorship functions and age-specific fecundity functions (expressed per day) for males and females in the bad habitat are given in the Appendix (Fig. A4) along with the survival and fecundity functions for males and females in the good habitat observed by Gerson et al. (1983) and Radwan and Bogacz (2000). Average longevity of adult fighters was 20.0 ± 4.3 (mean \pm SE) days and of adult scamblers 28.5 ± 5.3 days. This confirms previous results that scamblers live longer than fighters (Tables 1 and 2; Radwan and Bogacz 2000). The average, total lifetime egg production R_0 of females in the good habitat was 85.65 (Gerson et al. 1983) and in the bad habitat 3.25.

Hypopus induction and environmental determination of male morph expression

During this experiment, we did not observe hypopodes in mite populations in the good habitat. In the populations in the bad habitat 75 mites (including males and females) developed into a hypopus. The total number of males in the experiment was 1252 so that the overall probability that a mite would develop into a hypopus was estimated at (assuming a sex ratio of 1:1 [Gerson et al. 1983]): $75/(2 \times 1252) = 0.03$. We ran a generalized linear model with binomial errors to test the effect of male morph and dry period on the proportion of hypopodes in male populations in the bad habitat. Neither male morph ($\hat{p} = 0.69, t = 1.69, P = 0.09$), dry period ($\hat{p} = 0.21, t = 0.54, P = 0.59$), nor the interaction ($\hat{p} = -0.64, t = -1.21, P = 0.23$) had a significant effect on the proportion of hypopodes. Of the 46 hypopodes that were individually isolated, 25 developed into females and 21 into fighters (all survived to become adults). None of the hypopodes developed into a scrambler. A three-way analysis of deviance with binomial errors revealed that neither sire male morph (M; $\hat{p} = -0.06, t = -0.10, P = 0.92$), dry period (D; $\hat{p} = -0.02, t = \hat{p}0.05, P = 0.96$) nor habitat (H; $\hat{p} = -0.28, t = -0.57, P = 0.57$) affected the proportion of scamblers in the male population. None of the interactions were significant either (M \times D, $\hat{p} = 0.04, t = 0.06, P = 0.95$; M \times H, $\hat{p} = -0.47, t = -0.63, P = 0.53$; D \times H, $\hat{p} = -0.18, t = -0.28, P = 0.78$; M \times D \times H, $\hat{p} = 0.56, t = 0.61, P = 0.54$).

Perturbation analysis

The stochastic growth rate λ_s of the expected population size was lower for scamblers than fighters (although not necessarily significantly lower given the

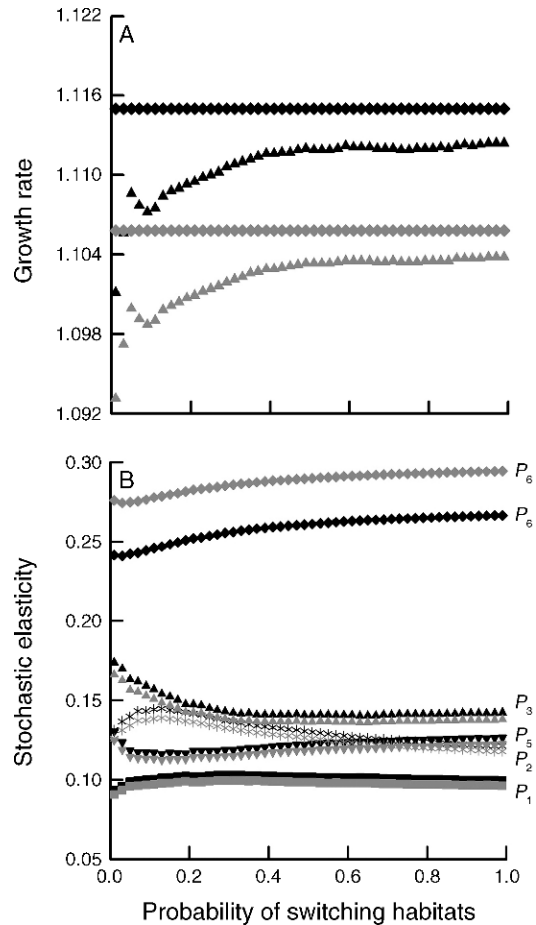


FIG. 2. (A) Stochastic growth rate λ_s (triangles) and asymptotic growth rate λ_A (diamonds) of fighters (black symbols) and scamblers (gray symbols) as a function of the probability of switching habitats (p). (B) Stochastic elasticities of λ_s (E_{ij}^S) for fighters (black symbols) and scamblers (gray symbols) with respect to the survival rates of eggs (P_1), larvae (P_2), protonymphs (P_3), tritonymphs (P_5), and adults (P_6). Elasticities of vital rates that were lower than 5% are not shown.

large amount of variation in, for example, longevity), irrespective of the probability of switching habitats (Fig. 2A), implying ultimate domination of fighters. The dominant eigenvalue λ_A of the mean (weighted arithmetic average) PPM of vital rates is equivalent to the commonly used asymptotic growth rate (Tuljapurkar et al. 2003). The difference (although not necessarily significant given the large amount of variation in, for example, longevity) between λ_s and λ_A was highest when the probability of switching habitats was lower than 0.3, implying that a long sequence of bad days is worse than occasionally occurring bad days (Fig. 2A). This region is associated with red noise where the autocorrelation of the habitat matrix is high and positive. Additionally, at very low values of p , λ_s of fighters was lower than the λ_A of scamblers, whereas the reverse was true for other values of p , implying that environmental variation can

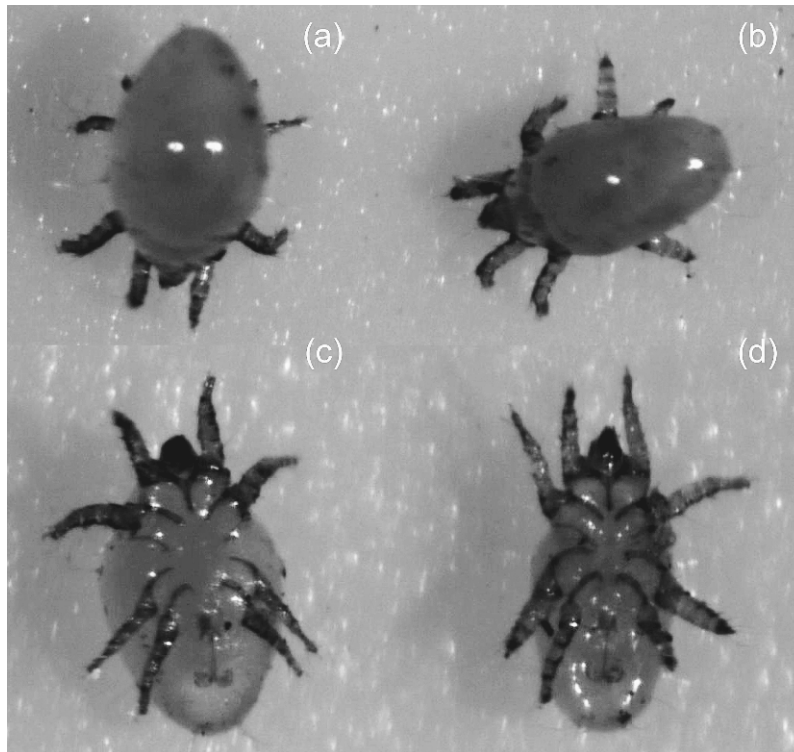


PLATE 1. (a, c) Top view and ventral view of a scrambler and (b, d) a fighter male bulb mite. Note that, in contrast to a scrambler, a fighter has a thickened third pair of legs, which it can use to kill rival males. Photos were taken at the same magnification. Photo credits: I. M. Smallegange.

be of crucial importance in concluding which morph would ultimately dominate in a population.

Next we explored the stochastic elasticity ($E_{ij}^{S\sigma}$) of λ_s to the perturbation of the vital rates of the different size classes, and the elasticity of λ_s with respect to the mean of each vital rate ($E_{ij}^{S\mu}$). The elasticity of λ_s with respect to the variance of each vital rate ($E_{ij}^{S\sigma}$) is the difference between $E_{ij}^{S\mu}$ and $E_{ij}^{S\sigma}$ and is not reported here. The methods that we use are such that if the mean of each vital rate is perturbed ($E_{ij}^{S\mu}$), there is no change in variance so that only changes in the mean value of vital rates contribute to λ_s (likewise, when the variance of each vital rate is perturbed [$E_{ij}^{S\sigma}$], the mean is kept fixed; Tuljapurkar et al. 2003). We only report elasticities greater than 0.05, and, because $E_{ij}^{S\mu}$ and $E_{ij}^{S\sigma}$ greater than 0.05 were highly correlated within vital rates ($\rho > 0.98$, $P < 0.001$), we focus on $E_{ij}^{S\mu}$. Survival of adults made the largest contribution to $E_{ij}^{S\mu}$, and its elasticity was higher for scramblers than for fighters (Fig. 2B). Survival of larvae, protonymphs, and tritonymphs made the next largest contributions to $E_{ij}^{S\mu}$, followed by the contribution of survival of eggs to $E_{ij}^{S\mu}$ (Fig. 2B). The latter elasticities were always slightly higher for fighters than for scramblers. The range of values of $E_{ij}^{S\mu}$ to the survival of eggs, larvae, protonymphs, tritonymphs and adults was largest in the red noise region (low values of p ; Fig.

2B). Elasticities of λ_s to the other vital rates were always lower than 0.05.

Comparing scrambler and fighter growth rates

The elasticity analyses revealed that the survival rate of adults (P_6) made the largest contribution to λ_s . To compare scrambler and fighter growth rates we explored how variation in P_6 of scramblers would affect the difference in λ_s between scramblers and fighters. As scramblers live longer than fighters (Radwan and Bogacz 2000, this study), this sensitivity analysis may also inform on the possibility of a trade-off between increased longevity as a scrambler (but low fighting ability), and increased fighting ability as a fighter (but reduced longevity). We conducted this sensitivity analysis for three probabilities of switching habitats, which are representative of the color of the environmental stochasticity: $p = 0.1$ (red noise), $p = 0.5$ (white noise), and $p = 0.9$ (blue noise). Perturbing P_6 in the good habitat PPM of scramblers revealed that an increase in P_6 up until unity did not result in equal λ_s for scramblers and fighters, irrespective of the probability of switching habitats (Fig. 3A). Perturbing P_6 in the bad habitat PPM of scramblers showed that an increase in adult survival rate of scramblers by at least 5% (depending on the probability of switching habitats) resulted in an equal λ_s of scramblers and fighters (Fig. 3A).

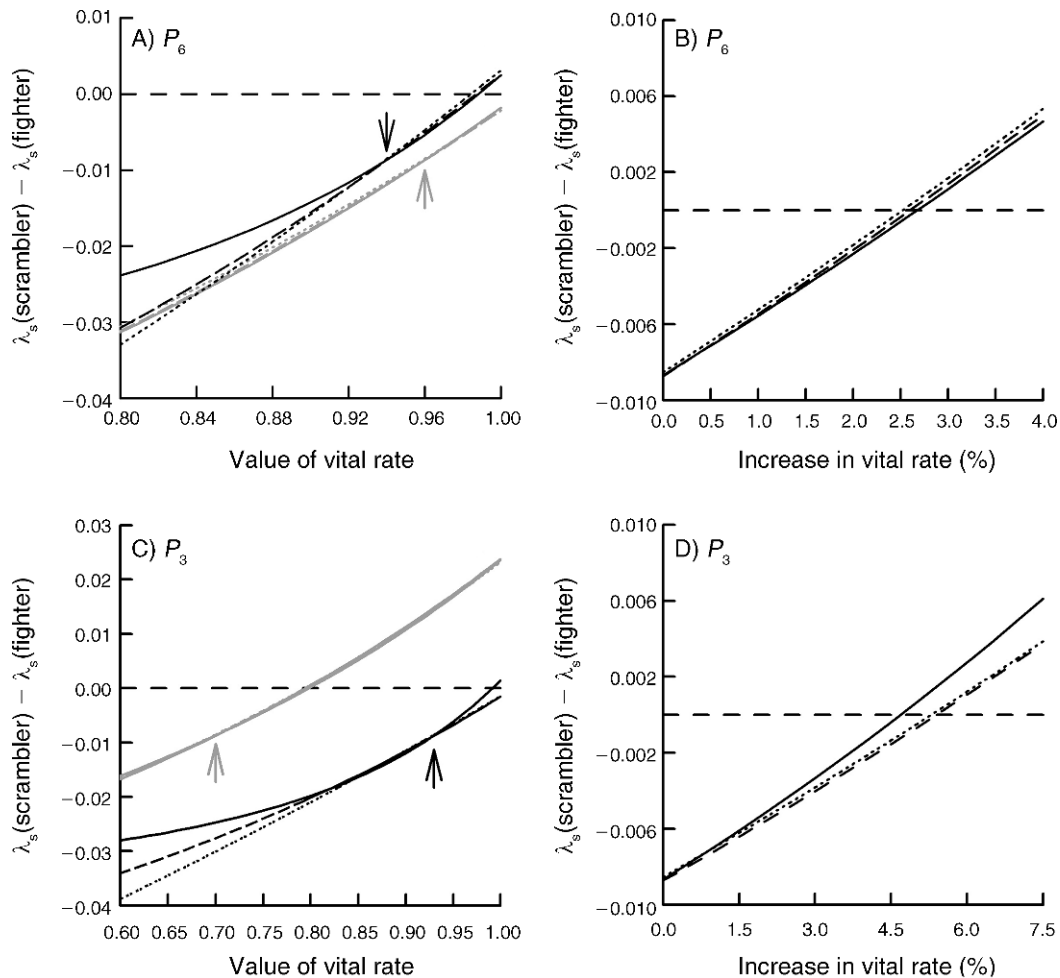


FIG. 3. The difference in the stochastic growth rate (λ_s) between scambler and fighters as (A) a function of increasing adult survival rate (P_6) of scambler and (C) as a function of increasing protonymph survival rate (P_3) of scambler. In panels A and C, gray lines denote perturbation of the vital rate in the good habitat population projection matrix (PPM), and black lines denote perturbation of the vital rate in the bad habitat PPM. The arrows denote actual values of each vital rate in the good and bad habitat PPM of scambler (gray and black arrow, respectively; Appendix). Panels B and D show the difference in λ_s between scambler and fighters as a function of the percentage increase in adult survival (P_6) and protonymph survival (P_3). Vital rates were increased by the same amount in both PPMs of scambler simultaneously. In all panels, different lines represent different probabilities of switching habitats (p): $p = 0.1$ (solid lines), $p = 0.5$ (dashed lines), and $p = 0.9$ (dotted lines), representing the color of the environmental stochasticity. The horizontal dashed line denotes zero difference between growth rates of scambler and fighters.

The next largest contribution to λ_s in the elasticity analyses was the survival rate of protonymphs (P_3). Again we investigated the relationship between variation in P_3 of scambler and the difference in λ_s between scambler and fighters. Perturbing P_3 in the good habitat PPM showed that a 26% increase in P_3 resulted in an equal λ_s for scambler and fighters (Fig. 3C). In contrast, a 7% increase in P_3 in the bad habitat PPM resulted in an equal λ_s of scambler and fighters but only at $p = 0.1$ (Fig. 3C). At other values of p , λ_s of scambler always remained lower than λ_s of fighters with increasing P_3 . Perturbing the two vital rates P_6 and P_3 in each PPM by the same amount revealed that an increase by at least 2.6% and 4.7% for P_6 and P_3 respectively, was required for λ_s of scambler to be equal to λ_s of fighters (Fig.

3B, D). Exploring each of these perturbations over the whole range of probabilities of switching habitats revealed that coexistence was restricted to certain colors of the environmental noise (Fig. 4).

Last, we assessed if any of the above perturbations of vital rates are biologically realistic. To this end we first increased average adult longevity by a biologically realistic amount, for example one standard error of the mean. This increased average adult longevity to 33.8 days in the bad habitat and to 52.0 days in the good habitat (Radwan and Bogacz 2000). The corresponding increase in P_6 was 2.8% and 3.1% (assuming that 50% of adults are alive after having been alive for half their longevity). In both cases the increase is higher than the 2.6% that is required for λ_s of scambler to be similar to

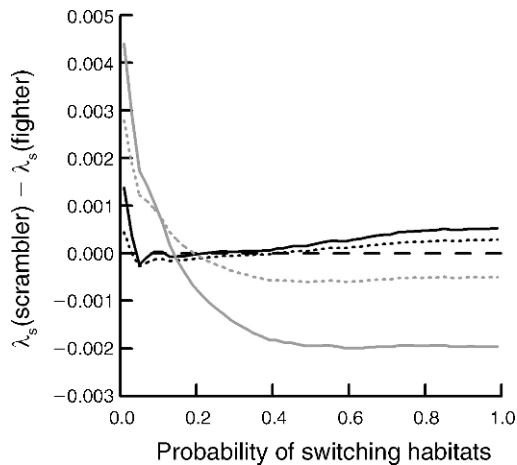


FIG. 4. The difference in the stochastic growth rate (λ_s) between scramblers and fighters with increasing probability of switching habitats. The lines denoting P_6 (in black) show perturbation by 5% in the bad habitat PPM of scramblers (solid line) and perturbation by 2.6% in both PPMs of scramblers (dotted line). The lines denoting P_3 (in gray) show perturbation by 7% in the bad habitat PPM of scramblers (solid line) and perturbation by 5% in both PPMs of scramblers (dotted line). The horizontal dashed line denotes zero difference between the growth rate of scramblers and fighters.

λ_s of fighters (Fig. 3B). For P_3 , an increase is not likely to be mediated through an increase in the longevity of protonymphs, but rather through an increase in the daily survival probability of an individual (σ). However, σ was already estimated at unity for scramblers in the good habitat. For scramblers in the bad habitat σ was 0.97, allowing a maximal increase of 3%. Increasing σ by 3% increased P_3 by 1.7%, which is lower than the 4.7% required for λ_s of scramblers to be equal to λ_s of fighters (Fig. 3D).

DISCUSSION

The existence of genetic variance in species populations is one of the central issues in evolutionary biology. We explored conditions for coexistence of genetically distinct morphs and hypothesized that *if* such coexistence occurs in different types of stochastic environments, then the coexisting morphs should have statistically indistinguishable long-run stochastic growth rates. We explored this premise for a heritable trait of the acarid bulb mite, combining stochastic demography with life-history experiments. Especially in acarids we might expect coexistence to be possible across a range of stochastic environments given that different populations of mites likely experience different environmental regimes. We observed that the stochastic growth rates of two genetically distinct morphs that differ considerably in their life history were equivalent across a range of stochastic environmental regimes. Additionally, the perturbation analysis showed that, across a range of environments, characterized by different frequencies and sequences of good and bad environmental conditions,

vital rates of mites do not need to vary much with changing frequency or density in order for coexistence to occur. Moreover, the change in vital rates required to increase the long-run growth rate of scramblers was within the 95% confidence interval around the point estimates, hence this change could not have been statistically detected. These results suggest that the coexistence of the two morphs requires weak stabilization operating on the two morphs (Adler et al. 2007). Overall, our results support applications of stochastic demographic models in environments that assume density or frequency dependence, illustrating that stochastic demography offers a powerful approach to identify and understand the circumstances under which genetic polymorphisms can be maintained in stochastic environments.

In the mite family Acaridae, male dimorphism (fighters, scramblers) exists in a number of species of at least three genera (*Sancassania*, *Rhizoglyphus*, *Schwiebia*; Woodring 1969). In some of these species the alternative reproductive phenotypes are genetically monomorphic and male morph expression is controlled by population density (Radwan 1993, 2001). Male morph expression in the bulb mite is partially genetically determined (Radwan 1995), and this is confirmed by our selection experiment. The threshold model is rooted in the science of human diseases where it is used to estimate heritability of susceptibility to disease (Falconer 1989): if liability (to catch a disease) is below a certain threshold the “normal” phenotype is expressed, whereas the “affected” phenotype is expressed if liability exceeds the threshold value. Heritability of liability is then calculated by comparing the “affected” population with the “normal” population (Falconer 1989). In our selection experiment we calculated the heritability of liability for both fighters and scramblers, where each was the “affected” phenotype with the other phenotype being “normal,” but assuming that the same liability and threshold underlies male morph expression. However, the response to selection in our experiment was asymmetrical with a higher estimated heritability in the scrambler lines. This could be a simple statistical artefact, although previous studies found a similar asymmetric response to selection (Radwan 1995, 2003) and attributed this to directional dominance for the alleles determining the fighter morph (Radwan 2003). We did not find evidence for an environmental influence on male morph expression. However, this could be due to low statistical power as, in the same experiment, we also did not find an effect of male sire morph on male morph expression. More work is required to understand the genetic architecture and environmental influence on male morph expression in bulb mites.

Why the two morphs coexist still puzzles biologists (Radwan 2007), mainly because scramblers always seem to be worse off. Unlike scramblers, fighters are able to attack and kill rival males (Radwan et al. 2000), and in small groups fighters are sometimes able to monopolize

access to females (in 15% of cases observed [Radwan and Klimas 2001]). The fact that the long-run stochastic growth rates of fighters and scambler were very similar across a wide range of stochastic environments suggests that only weak stabilizing mechanisms are required for their coexistence (Adler et al. 2007). This is supported by the fact that no experimental evidence of either strong density or frequency dependence has yet been found for bulb mites, at least in constant environments (Radwan and Klimas 2001). To unequivocally confirm if weak stabilization is required for the coexistence of these morphs in stochastic environments, as suggested by our experimental results, further experiments are required. These experiments should focus on testing the consequences of stabilization and fitness equivalence for coexistence of different genetic morphs as outlined by Adler et al. (2007). This might, however, be challenging given the fact that we found that the change in vital rates required to increase the long-run growth rate of scambler was within the 95% confidence interval around the point estimates. A more mechanistic understanding of why the two different morphs exist would also prove useful. Current understanding is that the morphs are partly genetically determined (Radwan 1995; this study), but the exact mechanism of morph expression has not yet been identified. Apart from classical (weak) frequency dependence, the dimorphism could also be maintained through what we term stochastic-environment-dependent selection. We observed that the relative fitnesses of the two morphs varied with the color of environmental noise so that fluctuations in the stochasticity of the environment could maintain the male dimorphism. This might, however, require a storage effect whereby individuals of the currently disadvantageous genotype survive until the next favorable episode of environmental noise (cf. Chesson 1994, Ellner and Hairston 1994). Radwan (2007) suggested that scambler are “making the best of a bad job,” but this assumes that fighter legs are costly to develop, that mites in poor condition refrain from developing fighter legs, and that male condition is heritable (Radwan 2007). None of these assumptions have been tested or verified (Radwan 2007). As yet, the only positive difference in a life-history trait between scambler and fighters that has been found is that scambler live longer than fighters (Radwan and Bogacz 2000). Interestingly, adult survival turned out to be the vital rate that played the dominant role in our investigation on the coexistence of two genetically distinct morphs in stochastic environments.

The stochastic growth rates of scambler and fighters based on our point estimates of the vital rates revealed that, in the long-run, bulb mite populations would be dominated by fighters (because their stochastic growth rate was highest). Unfortunately, the studies from which we collected most of the life table data did not report errors around the parameter estimates so we could not conduct our analyses using distributions of vital rates.

We did, however, know the error distribution of adult longevity. An increase in scambler adult longevity within one standard error of the mean (and a corresponding increase in scambler adult survival rate; the rate to which λ_s was most sensitive in perturbation analyses) was sufficient to equalize the stochastic growth rates of scambler and fighters across different types of stochastic environments. In variable environments, increasing chances of survival at the expense of other vital rates could increase fitness, as risks are spread across uncertain environmental conditions. Metcalf and Koons (2007) indeed found for semelparous life-histories that allocation towards survival, even at the cost of reduced fecundity, is favored in more variable environments. This might play a role in the evolution of scambler mites: their fecundity rate was estimated lower than that of fighters, but their adult survival rate was higher, as a result of which their stochastic growth rate was comparable to that of fighters. Even more so, a slight increase in scambler longevity resulted in a higher stochastic growth rate of scambler than fighters at high probabilities of switching habitats (Fig. 4).

In conclusion, the life tables of fighters and scambler were constructed in a frequency- and density-independent environment. The magnitude of stabilizing mechanisms such as density or frequency dependence necessary to ensure long-term coexistence of these two morphs likely is small, as the stochastic growth rates were statistically indistinguishable under a wide variety of environmental conditions. Therefore, we advocate the application of stochastic demographic models to identify and understand problems such as the coexistence and maintenance of different genetic morphs in stochastic environments. Stochastic demographic theory has provided tools to study how environmental variability affects population growth and fitness (Boyce et al. 2006). Here we show how this first experimental application of stochastic demography using laboratory populations opens up more opportunities for stochastic demographic research (Smallegange and Coulson 2009). For example, hypotheses on the consequences of altering the temporal distribution of vital rates on the long-run stochastic growth rate could be experimentally tested, either by imposing different mortality regimes or by altering the environment. Such experiments may also inform on the consequences of temporal correlation of environmental variation on time to extinction (Inchausti and Halley 2003, Boyce et al. 2006, Benaïm and Schreiber 2009). Finally, laboratory populations are ideal model systems to trial the importance of evolutionary analysis in stochastic demography and to push forward our understanding of eco-evolutionary dynamics in stochastic environments.

ACKNOWLEDGMENTS

We thank Izabela Lesna for providing the mites and Maurice Sabelis, Arpat Ozgul, and Aurelio Malo for constructive comments. I. M. Smallegange was sponsored by the Nether-

lands Organisation for Scientific Research (Rubicon Fellowship), and T. Coulson acknowledges Wellcome Trust funding.

LITERATURE CITED

- Adler, P. B., J. HilleRisLambers, and J. M. Levine. 2007. A niche for neutrality. *Ecology Letters* 10:95–104.
- Benaïm, M., and S. J. Schreiber. 2009. Persistence of structured populations in random environments. *Theoretical Population Biology* 76:19–34.
- Boyce, M. S., C. V. Haridas, and C. T. Lee. and the NCEAS Stochastic Demography Working Group. 2006. Demography in an increasingly variable world. *Trends in Ecology and Evolution* 21:141–148.
- Capua, S., and U. Gerson. 1983. The effects of humidity and temperature on hypopodial molting of *Rhizoglyphus robini*. *Entomologia Experimentalis et Applicata* 34:96–98.
- Caswell, H. 2001. Matrix population models. Sinauer Associates, Sunderland, Massachusetts, USA.
- Chesson, P. L. 1994. Multispecies competition in variable environments. *Theoretical Population Biology* 45:227–276.
- Chesson, P. L. 2000. Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics* 31: 343–366.
- Cohen, J. E. 1977. Ergodicity of age structure in populations with Markovian vital rates. III. Finite-state moments and growth rates: an illustration. *Advances in Applied Probability* 9:462–475.
- Diaz, A., K. Okabe, C. J. Eckenrode, M. G. Villani, and B. M. O'Connor. 2000. Biology, ecology, and management of the bulb mites of the genus *Rhizoglyphus* (Acari: Acaridae). *Experimental and Applied Acarology* 24:85–113.
- Ellner, S., and N. G. Hairston. 1994. Role of overlapping generations in maintaining genetic variation in a fluctuating environment. *American Naturalist* 143:403–417.
- Falconer, D. S. 1989. Introduction to quantitative genetics. Third edition. John Wiley and Sons, New York, New York, USA.
- Gerson, U., S. Capua, and D. Thorens. 1983. Life history and life tables of *Rhizoglyphus robini* Claparede (Acari: Astigmata: Acaridae). *Acarologia* 24:439–448.
- Gross, M. R. 1996. Alternative reproductive strategies and tactics: diversity within sexes. *Trends in Ecology and Evolution* 11:92–98.
- Inchausti, P., and J. Halley. 2003. On the relation between temporal variability and persistence time in animal populations. *Journal of Animal Ecology* 72:899–908.
- Lesna, I., M. Sabelis, and C. Conijn. 1996. Biological control of the bulb mite, *Rhizoglyphus robini*, by the predatory mite, *Hypoaspis aculeifer*, on lilies: predator–prey interactions at various spatial scales. *Journal of Applied Ecology* 33:369–376.
- Metcalf, C. J. E., and D. N. Koons. 2007. Environmental uncertainty, autocorrelation and the evolution of survival. *Proceedings of the Royal Society B* 274:2153–2160.
- Metcalf, C. J. E., and S. Pavard. 2007. Why evolutionary biologists should be demographers. *Trends in Ecology and Evolution* 22:205–212.
- Metz, J. A. J., R. M. Nisbet, and S. A. H. Geritz. 1992. How should we define “fitness” for general ecological scenarios? *Trends in Ecology and Evolution* 7:198–202.
- Radwan, J. 1993. The adaptive significance of male polymorphism in the acarid mite *Caloglyphus berlessei*. *Behavioral Ecology and Sociobiology* 33:201–208.
- Radwan, J. 1995. Male morph determination in 2 species of acarid mites. *Heredity* 74:669–673.
- Radwan, J. 2001. Male morph determination in *Rhizoglyphus echinopus* (Acaridae). *Experimental and Applied Acarology* 25:143–149.
- Radwan, J. 2003. Heritability of male morph in the bulb mite, *Rhizoglyphus robini* (Astigmata, Acaridae). *Experimental and Applied Acarology* 29:109–114.
- Radwan, J. 2007. Sexual selection and conflict in the bulb mite, *Rhizoglyphus robini* (Astigmata: Acaridae). *Experimental and Applied Acarology* 42:151–158.
- Radwan, J., and I. Bogacz. 2000. Comparison of life-history traits of the two male morphs of the bulb mite, *Rhizoglyphus robini*. *Experimental and Applied Acarology* 24:115–121.
- Radwan, J., M. Czyż, M. Konior, and M. Kołodziejczyk. 2000. Aggressiveness in two male morphs of the bulb mite *Rhizoglyphus robini*. *Ethology* 106:53–62.
- Radwan, J., and M. Klimas. 2001. Male dimorphism in the bulb mite, *Rhizoglyphus robini*: fighters survive better. *Ethology, Ecology and Evolution* 12:69–79.
- Shuster, S., and S. M. Wade. 1991. Equal mating success among male reproductive strategies in a marine isopod. *Nature* 350:608–610.
- Slatkin, M. 1978. On the equilibration of fitnesses by natural selection. *American Naturalist* 112:845–859.
- Smallegange, I. M., and T. Coulson. 2009. Unifying ecological and evolutionary dynamics through experimental stochastic demography. *Israel Journal of Ecology and Evolution* 55: 199–205.
- Tuljapurkar, S. 1990. Population dynamics in variable environments. Springer, New York, New York, USA.
- Tuljapurkar, S., C. C. Horvitz, and J. B. Pascarella. 2003. The many growth rates and elasticities of populations in random environments. *American Naturalist* 162:489–502.
- Woodring, J. P. 1969. Observations on the biology of six species of acarid mites. *Annals of the Entomological Society of America* 62:102–108.

APPENDIX

Experimental designs and population projection matrices (*Ecological Archives* E092-063-A1).